Appendix 2. Description of the Population Analysis (P. Wade)

Methods

The methods used are very similar to those in Wade (1994) and Wade (in press_a). Wade (1994) used an identical population model and nearly identical Bayesian methods to estimate depletion levels of both northeastern offshore spotted dolphins and eastern spinner dolphins. Wade (in press_a) contains a similar analysis of northeastern offshore spotted dolphins using identical statistical methods, but with a non-age-structured model.

Other analyses fitting population models to data using nearly identical statistical methods can be found in Taylor *et al*. (1996), Wade (in press_b) and Wade (submitted). Somewhat similar Bayesian analyses of cetacean populations can be found in Givens *et al*. (1993, 1995), Raftery *et al*. (1995), and Punt and Butterworth (1997). A similar fisheries assessment is McAllister *et al*. (1994), and an overview of Bayesian methods in fisheries assessment is Punt and Hilborn (1997).

Data

A population model was projected from 1958 to 1998 and fit to available abundance data. Abundance estimates are available from research vessel surveys in ten years from 1979 to 1998. Estimates used from 1979 to 1990 were from Wade (1994), with an additional estimate available for 1998 (Gerrodette, 1999). Indices of abundance from data collected on tuna vessels (TVOD) are available for 23 years, from 1975 to 1997 (Anganuzzi and Buckland 1993, C. Lennert, pers. comm.). Log-normal likelihoods were used for both series of abundance estimates. The TVOD data were scaled to absolute abundance using a scale parameter, a.

Fisheries mortality estimates are available for every year from 1959 to 1997 (Table A1 and Table A2). For both stocks, estimates for 1959-72 were from Wade (1995). For the northeastern offshore spotted dolphin, estimates for 1973-1997 were from the IATTC. For the eastern spinner dolphin, estimates for 1973-1978 were from Wahlen (1986), as modified in Wade (1993). Estimates for 1979-1997 were from the IATTC. Estimates of fisheries mortality for 1998 are not yet available; therefore, mortality in 1998 was assumed to be equal to mortality in 1997, with a small amount of variability (CV = 0.10) specified in this assumed 1998 mortality to account for uncertainty in its actual level. The sampling errors of the mortality estimates was assumed to be log-normal. Additionally, the sampling errors of the mortality estimates from 1959-72 were assumed to be correlated, because mortality-per-set rates were pooled across that time period (Wade 1995).

Population model

The model used was an age-structured density-dependent model in the form of a Leslie matrix (Breiwick et al. 1984). Parameters of the model were juvenile survival (s_j), adult survival (s_a), maximum fecundity rate (f_{max}), age of sexual maturity (*asm*), age of transition to adult survival (*ia*), maximum age (*iw*), and equilibrium population size (N_{eq}). This model was identical to a usual Leslie matrix model, except that the fecundity term was density-dependent with a form similar to the generalized-logistic with a shape parameter (z) which determines the maximum net productivity level:

$$f_t = f_0 + (f_{max} - f_0)\left(1 - \left(\frac{N_t}{N_{eq}}\right)^z\right) \tag{1}$$

where f_t = the realized fecundity in year t, f_{max} = the maximum fecundity rate, and f_0 = fecundity at a net recruitment of zero, which can be solved directly from the other parameters (Breiwick et al. 1984).

The population was projected as

$$N_{t+1} = \mathrm{A}_t N_t - M_t \tag{2}$$

where N_t = vector of population size of each age class at time t, A_t = the Leslie matrix in year t, and M_t = vector of age-specific additional mortality at time t. The maximum population growth rate (r_{max}) was calculated as λ_{max}-1, where λ_{max} was the λ associated with the Leslie matrix with fecundity equal to f_{max}.

The population size was assumed to be equal to N_{eq} in 1958, and to be in the stable age distribution associated with the equilibrium Leslie matrix (where the fecundity rate was equal to f_0, the fecundity rate at equilibrium or zero population growth). In each year, (1) the population was projected using the model, (2) the additional mortality was subtracted, and (3) the model population size was compared to the abundance data (if available in that year).

Difference in the population growth rate

An additional parameter (μ) was estimated representing a potential difference in the population growth rate from 1992 to 1998 relative to 1975-1991. After estimating r_{max} from the abundance data from 1975-1991, the population was then projected on through 1998 with the expected realized growth rate, given the estimated model parameters, and estimated depletion level (population level relative to N_{eq}). Any difference between the expected model trajectory and the estimated 1992-1998 population trajectory (as fit to the 1992-1998 abundance data) represents an estimate of a change in the population growth rate. An additional parameter (μ) was specified to represent this potential change from the expected population growth rate from 1992 to 1998, acting through additional mortality (mortality in addition to that due to parameters s_j and s_a). In the model trajectory, prior to 1992, additional mortality was from only the estimated fisheries mortality. In 1992 and later years, additional mortality was equal to $M_t + \mu N_t$, where M_t was the observed estimated mortality in year t, and N_t was the model population size in year t. Therefore, μ represents an estimate of the difference between the expected population growth rate and the observed population growth rate in the years 1992-1998. A total additional mortality rate was calculated as $\mu_{tot} = (M_t + \mu N_t)/N_t = (M_t/N_t) + \mu$.

The estimation of r_{max} from the abundance data from 1975-1991, and then the estimation of μ conditioned on that estimate of r_{max}, could be done sequentially in two separate steps. However, it was simpler to estimate both in a single analysis, by projecting the population model through 1998, and including the contributions to the likelihood from the 1992-1998 abundance data to the total likelihood.

Age-specific selectivities

Age-specific selectivities were calculated using an iterative convergence routine, such that the age structure of the fisheries mortality in 1984 was equal to the smoothed observed age distribution of the kill from 1974-1992 shown in Wade (1994, Fig. 6.3).

Bayesian methods

The Bayesian joint posterior distribution was approximated using the SIR routine (Smith and Gelfand 1992). Prior distributions were specified for the eight parameters N_{eq}, s_a, s_j, f_{max}, z, asm, a, and μ (see below). The parameters *ia* and *iw* were set to fixed values (see below). Marginal probability distributions were calculated for all the estimated parameters. In particular, a probability distribution for the decision quantity, the ratio μ/r_{max}, was calculated. The cumulative probability this ratio was greater than 1.0, 0.5, 0.25, and 0.1 was also calculated.

Likelihood function

The likelihood function for the parameters in a population model, given a time-series of abundance estimates, were calculated according to the methods reported in de la Mare (1986). In any single year, the likelihood of an observed abundance estimate $N_{abun}(t)$ given a specified model population size $N_{model}(t)$ is straight forward; it is the likelihood function defined by the assumed sampling distribution of the abundance estimate. The sampling distribution of the abundance estimates was assumed to be a Log-normal distribution with point estimate $N_{abun}(t)$:

$$L(N_{abun}(t)|N_{model}(t), \sigma(t)) = \frac{1}{\sqrt{2\pi}\,\sigma(t)} e^{-\frac{1}{2}\left(\frac{\ln N_{abun}(t) - \ln N_{model}(t)}{\sigma(t)}\right)^2} \quad (3)$$

σ was approximated by the CV of the abundance estimate in year t. For the TVOD, the parameter a was used to scale the model abundance to the TVOD data. Therefore, the likelihood for TVOD data was

$$L(N_{TVOD}(t)|N_{model}(t), \sigma(t), a) = \frac{1}{\sqrt{2\pi}\,\sigma(t)} e^{-\frac{1}{2}\left(\frac{\ln N_{TVOD}(t) - (\ln(a \cdot N_{model}(t)))}{\sigma(t)}\right)^2} \quad (4)$$

The total likelihood given the data is the product series of all the individual likelihoods.

Prior distributions

Prior distributions were specified for the eight fundamental parameters of the model (Table A3). Estimates of the age of sexual maturity and calving interval for spotted dolphins are in Myrick *et al.* (1986). Although these estimates were made for the previous stock definition, the northern offshore stock, a check of location records confirmed that nearly all examined animals were from within the northeastern stock area, as well (S. Chivers, pers. comm., as cited in Wade 1994). Myrick *et al.* (1986) reports two estimates of *asm*, 10.7 (95% CI 10.36, 11.04) and 12.2 (11.76, 12.64), corresponding to estimated ages from teeth read by two different people. These two estimates were combined into a single distribution covering the extremes of the two intervals, giving an estimate of 11.45 (10.36, 12.64), using a normal distribution as a large sample approximation.

Myrick et al. (1986) estimate the pregnancy rate at 0.33, corresponding to a calving interval of 3 years. This corresponds to a fecundity rate of 0.167 females per female. This can serve as a lower bound to a maximum fecundity rate. Lactation has been estimated to be at least 1 year (Perrin and Hohn, 1994). Only a small fraction of mature females (6%) have been found to be simultaneously lactating and pregnant (Chivers and Myrick 1993), suggesting a one-year calving interval is implausible. Offshore spotted dolphins in the eastern tropical Pacific have only a weak seasonal signal in birth-pulse, so a minimum calving interval less than 2 years is plausible. 1.5 years was chosen as a reasonable lower bound on calving interval, corresponding to an upper bound on maximum fecundity of 0.333 females per female. Therefore, a uniform prior from 0.167 to 0.333 was specified for the maximum fecundity rate.

No data are available on spotted dolphin survival rates in the eastern tropical Pacific. A uniform prior on 0.80 to 0.98 was specified for the juvenile survival rate. The age of transition to the adult survival rate was fixed at 9 (the ninth age class), and the maximum age class was specified as 40 (the oldest aged animal was 39 years old, Chivers and Myrick 1993). A uniform prior distribution for adult survival, in combination with the above specified prior distributions, results in an implied prior distribution for r_{max} that is not uniform, but is heavily weighted to very low values below 0.01. r_{max} was one of the output quantities of interest, and it was considered better to have a nearly non-informative prior specified for it. Therefore, a truncated normal distribution with mean 0.991, s.e. .02, was specified for s_a which results in a prior distribution for r_{max} that is nearly uniform. It was truncated at 0.998, creating a prior distribution for s_a that was essentially half-normal. This is in keeping with the general understanding that long-lived mammals that become sexually mature at 11 years would be expected to have high adult survival rates.

A uniform prior was specified for N_{eq} from 2300. to 5900. This range was specified as there was virtually zero posterior probability for N_{eq} at either end of this range. A uniform prior distribution was specified for *z* from 1.0 to 11.2, corresponding to maximum net productivity levels (MNPL) in a generalized logistic model from 50% to 80% of N_{eq}, which is considered a plausible range for MNPL in marine mammals (Taylor and DeMaster 1993). A uniform prior was also specified for the TVOD scale parameter *a* and for the parameter μ such that there was virtually zero posterior probability at either end of the specified ranges.

Prior distributions were similarly set for the eastern spinner dolphin (Table A3). *asm* has been estimated to be approximately 10 years (S. Chivers, pers. comm., as cited in Wade 1993). No standard error was given, but the methods were similar to those used for spotted dolphins in Myrick et al (1986). A conservative standard error of 1.0 was assumed, approximately twice as large as the standard error resulting for the estimate for spotted dolphins. Calving interval in spinner dolphins has similarly been observed to be 3 years (Perrin and Gilpatrick 1994), so identical values were used for f_{max}. Because of the younger *asm*, a slightly lower prior distribution for s_a was specified, again to give a relatively non-informative prior distribution for r_{max}. The age of transition to the adult survival rate was fixed at 8 (the eight age class), and the maximum age class was specified as 40.

The decision criteria were expressed in terms of the parameters or output quantities of the population model. These values for the decision criteria thresholds are specified in Table A4.

Results

Northeastern offshore spotted dolphin

Estimates of the eight parameters from the analysis of northeastern offshore spotted are in Table A5. Estimates of the output quantities of interest, which are functions of the eight parameters, are also presented in Table A5. The point estimate of r_{max} is 0.015, or about 1.5% population growth per year. The point estimate of μ is 0.038, or 3.8% of the population per year. The quantity μ_{tot}, which includes the estimated observed fisheries mortality, is slightly higher at 4.1%. Because μ is greater than r_{max}, this implies that the population declined from 1991 to 1998, which can be seen from a comparison of the posterior means for population size in those years (722. versus 582.), and from the trajectory itself (Fig. 1). This decline is consistent with the TVOD trend data over this time period.

The decision criteria probabilities are presented in Table A6. Each of these probabilities exceeds the specified acceptable levels of 0.01, 0.05, and 0.50. Therefore, the difference between the expected and observed population growth rate from 1992-1998 is considered to be too high.

Eastern spinner dolphin

Estimates of the eight parameters and output quantities from the analysis of the eastern spinner dolphin are in Table A7. The point estimate of r_{max} and μ are nearly the same (0.017 versus 0.016). The point estimate of the quantity μ_{tot} (0.017), which includes the estimated observed fisheries mortality, is identical to the estimate of r_{max}. However, the distribution for μ_{tot} has a longer tail at the upper end, meaning that there is substantial probability that μ_{tot} is greater than r_{max}. Because estimated values of μ_{tot} are similar to estimated values for r_{max}, this implies that the population was nearly stable or slightly declined from 1991 to 1998, which can be seen from a comparison of the posterior means for population size in those years (636. versus 623.) and from the trajectory (Fig. 2). Again, this result is consistent with the TVOD trend data over this time period.

The decision criteria probabilities are presented in Table A8. Each of these probabilities exceeds the specified acceptable levels of 0.01, 0.05, and 0.50. Therefore, the difference between the expected and observed population growth rate from 1992-1998 is considered to be too high.

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Appendix 2 (continued).

Table A1. Northeastern offshore spotted dolphin. Mortality is the estimated fisheries mortality in each year (mortality in 1998 was assumed to be equal to mortality in 1997). Abundance is the estimated abundance in each of 10 years from research vessel surveys. TVOD is the estimated trend index in each of 23 years from tuna vessel observer data. CV is the coefficient of variation of each estimate.

Year	Mortality	CV	Abundance	CV	TVOD	CV
1959	15900.	0.530				
1960	344000.	0.520				
1961	366000.	0.480				
1962	141000.	0.420				
1963	158200.	0.360				
1964	272300.	0.280				
1965	318500.	0.290				
1966	244100.	0.220				
1967	171800.	0.230				
1968	161200.	0.220				
1969	271500.	0.220				
1970	218700.	0.220				
1971	111300.	0.220				
1972	168100.	0.170				
1973	49900.	0.180				
1974	37400.	0.110				
1975	49400.	0.180			1539000.	0.19
1976	20400.	0.230			1581000.	0.20
1977	5900.	0.120			1523000.	0.17
1978	4200.	0.200			1187000.	0.19
1979	4800.	0.170	1031000.	0.36	1432000.	0.20
1980	6500.	0.150	438000.	0.46	1348000.	0.19
1981	8100.	0.190			976000.	0.12
1982	9300.	0.170	608000.	0.34	1054000.	0.14
1983	2400.	0.270	937000.	3.59	532000.	0.22
1984	7800.	0.190			1027000.	0.23
1985	26000.	0.120			1394000.	0.13
1986	52000.	0.160	318000.	0.28	1401000.	0.13
1987	35400.	0.120	490000.	0.22	1067000.	0.06
1988	26600.	0.100	1220000.	0.31	1159000.	0.12
1989	28900.	0.110	1445000.	0.26	1188000.	0.11
1990	26600.	0.110	407000.	0.46	1072000.	0.07
1991	9000.	0.110			1174000.	0.08
1992	4600.	0.070			1282000.	0.07
1993	1143.	0.080			911000.	0.08
1994	935.	0.070			895000.	0.07
1995	952.	0.000			913000.	0.07
1996	818.	0.000			910000.	0.06
1997	721.	0.000			927000.	0.06
1998	721.	0.100	1011000.	0.26		

Appendix 2 (continued).

Table A2. Eastern spinner dolphin. Mortality is the estimated fisheries mortality in each year (mortality in 1998 was assumed to be equal to mortality in 1997). Abundance is the estimated abundance in each of 10 years from research vessel surveys. TVOD is the estimated trend index in each of 23 years from tuna vessel observer data. CV is the coefficient of variation of each estimate.

Year	Mortality	CV	Abundance	CV	TVOD	CV
1959	6500.	0.470				
1960	138400.	0.470				
1961	153500.	0.430				
1962	62200.	0.400				
1963	69400.	0.370				
1964	112700.	0.340				
1965	132500.	0.340				
1966	107800.	0.330				
1967	72200.	0.330				
1968	65700.	0.330				
1969	110400.	0.350				
1970	104500.	0.330				
1971	60100.	0.320				
1972	88500.	0.320				
1973	18400.	0.160				
1974	17800.	0.110				
1975	17100.	0.110			670000.	0.43
1976	14700.	0.120			544000.	0.34
1977	1800.	0.120			494000.	0.28
1978	1100.	0.110			428000.	0.36
1979	1500.	0.240	409000.	0.43	323000.	0.57
1980	1100.	0.200	312000.	2.38	381000.	0.31
1981	2300.	0.280			222000.	0.54
1982	2600.	0.330	146000.	0.76	212000.	0.48
1983	700.	0.380	583000.	1.61	410000.	0.32
1984	6000.	0.520			375000.	0.37
1985	8900.	0.160			587000.	0.23
1986	19400.	0.190	378000.	0.53	590000.	0.20
1987	10400.	0.110	505000.	0.41	363000.	0.28
1988	18800.	0.090	1067000.	0.37	717000.	0.15
1989	15200.	0.110	855000.	0.49	389000.	0.18
1990	5400.	0.180	320000.	0.59	358000.	0.21
1991	5900.	0.130			358000.	0.18
1992	2794.	0.060			410000.	0.22
1993	821.	0.080			295000.	0.18
1994	743.	0.110			408000.	0.21
1995	654.	0.000			538000.	0.15
1996	450.	0.000			483000.	0.29
1997	391.	0.000			439000.	0.29
1998	391.	0.100	1158000.	0.34		

Appendix 2 (continued).

Table A3. Prior distributions for the parameters. Unif is a uniform distribution, Nrml is a normal distribution, trunc is truncated.

Parameter	northeastern spotted	eastern spinner
N_{eq}	Unif(2300, 5900.)	Unif(500, 3300.)
s_a	Nrml(0.991, .02), trunc(0.92, 0.998)	Nrml(0.99, .02), trunc(0.92, 0.995)
s_j	Unif(0.80, 0.98)	Unif(0.80, 0.98)
f_{max}	Unif(0.167, 0.333)	Unif(0.167, 0.333)
z	Unif(1.0, 11.2)	Unif(1.0, 11.2)
asm	Grouped Nrml(11.45, 0.56)	Grouped Nrml(10.0, 0.1)
a	Unif(0.90, 2.15)	Unif(0.3, 1.2)
μ	Unif(0.0, 0.1)	Unif(0.0, 0.08)
ia	9	8
iw	40	40

Table A4. Decision criteria thresholds. μ is the difference in the observed population growth rate from 1992-1998 from the expected rate as estimated from 1975-1991 abundance data. r_{max} is the maximum population growth rate, estimated from the fit of the model to the 1975-1991 abundance data. μ is considered unacceptable if any of these conditions are met.

(1) Prob($\mu > r_{max}$)	> 0.010
(2) Prob($\mu > 0.5*r_{max}$)	> 0.050
(3) Prob($\mu > 0.25*r_{max}$)	> 0.500

Table A5. Parameters and output quantities for the northeast offshore spotted dolphin. Mean is the mean of the posterior distribution. 2.5th and 97.5th are the respective percentiles of the posterior distribution. N_{eq}, N_{91}, and N_{98} are all in thousands of animals.

Parameter	Mean	2.5th	97.5th
N_{eq}	4039.	3063.	5164.
s_a	0.987	0.962	0.998
s_j	0.868	0.819	0.921
f_{max}	0.236	0.170	0.323
z	5.57	1.14	10.87
asm	11.65	11.00	13.00
a	1.502	1.224	1.823
μ	0.038	0.015	0.062

Output quantities	Mean	2.5th	97.5th
N_{91}	722.	581.	886.
N_{98}	582.	468.	729.
N_{98}/K	0.148	0.108	0.195
r_{max}	0.015	0.004	0.027
μ/r_{max}	2.948	1.453	6.102
μ_{tot}	0.041	0.017	0.066
μ_{tot}/r_{max}	3.152	1.544	6.512

Appendix 2 (continued).

Table A6. Decision criteria probabilities for the northeast offshore spotted dolphin.

(1) Prob($\mu > r_{max}$)	= 0.996
(2) Prob($\mu > 0.5*r_{max}$)	= 0.9988
(3) Prob($\mu > 0.25*r_{max}$)	= 0.9994

Table A7. Parameters and output quantities for the eastern spinner dolphin. Mean is the mean of the posterior distribution. 2.5th and 97.5th are the respective percentiles of the posterior distribution. N_{eq}, N_{91}, and N_{98} are all in thousands of animals.

Parameter	Mean	2.5th	97.5th
N_{eq}	1913.	1348.	2557.
s_a	0.976	0.947	0.994
s_j	0.848	0.803	0.923
f_{max}	0.240	0.170	0.323
z	5.82	1.20	10.91
asm	10.07	8.00	12.00
a	0.725	0.517	0.998
μ	0.016	0.001	0.052
Output quantities	**Mean**	**2.5th**	**97.5th**
N_{91}	636.	443.	882.
N_{98}	623.	420.	891.
N_{98}/K	0.340	0.215	0.524
r_{max}	0.017	0.003	0.036
μ/r_{max}	1.482	0.041	5.155
μ_{tot}	0.017	0.001	0.055
μ_{tot}/r_{max}	1.582	0.078	5.463

Table A8. Decision criteria probabilities for the eastern spinner dolphin.

(1) Prob($\mu > r_{max}$)	= 0.440
(2) Prob($\mu > 0.5*r_{max}$)	= 0.690
(3) Prob($\mu > 0.25*r_{max}$)	= 0.848

Figure 1. Model population trajectory and abundance data for the northeastern offshore spotted dolphin. Median model trajectory is the median model population size in each year from the posterior distribution. Expected trajectory is the expected model trajectory using r_{max} estimated from 1975-91 data, with μ set to 0.0. Abundance estimates are the research vessel abundance estimates. Scaled TVOD are the Tuna Vessel Observer Data trend estimates, scaled to absolute abundance by the estimated parameter *a*..

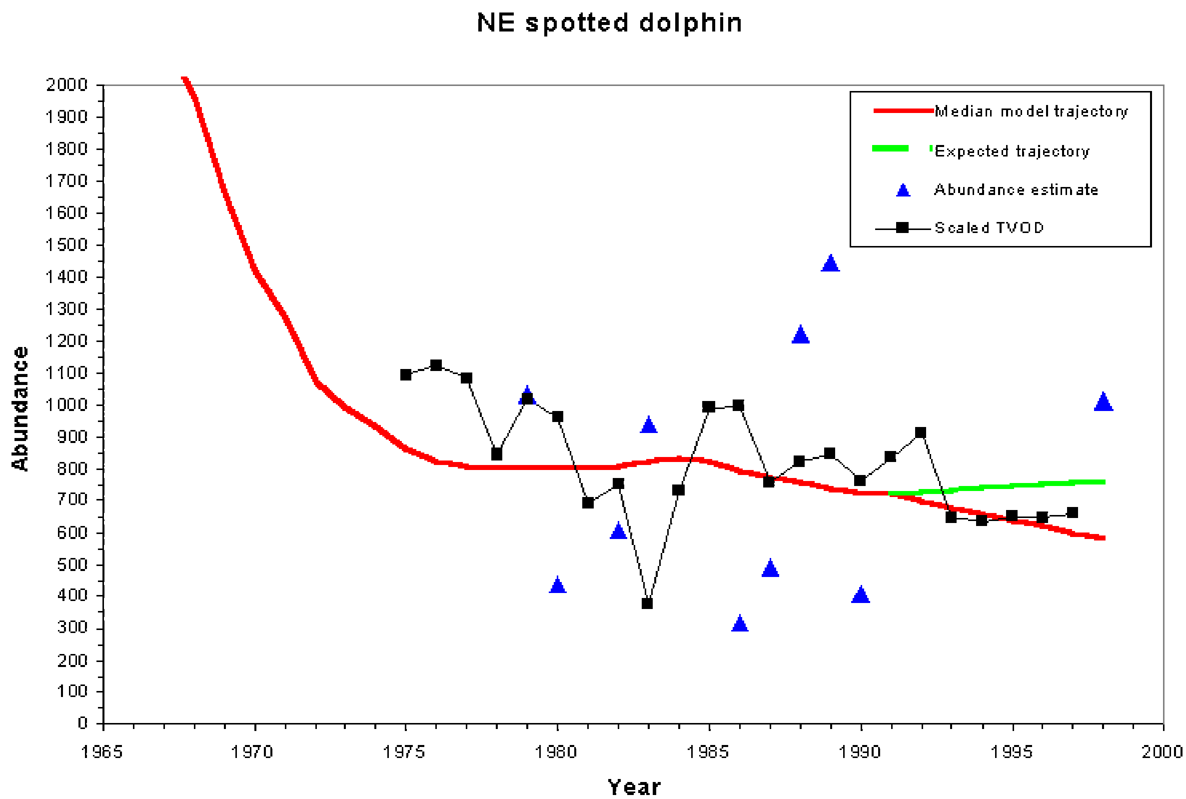

Figure 2. Model population trajectory and abundance data for the eastern spinner dolphin. Median model trajectory is the median model population size in each year from the posterior distribution. Expected trajectory is the expected model trajectory using r_{max} estimated from 1975-91 data, with set to 0.0. Abundance estimates are the research vessel abundance estimates. Scaled TVOD are the Tuna Vessel Observer Data trend estimates, scaled to absolute abundance by the estimated parameter *a*.